

XXXII.—*The Pelagic Fauna of Freshwater Lakes.*

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IN the years 1860–1870 the Scandinavian naturalists discovered a peculiar fauna, consisting essentially of swimming Entomostraca, which inhabits the pelagic region of lakes. I will endeavour to give a brief summary of this chapter of general zoology, which has been of late years repeatedly investigated, and has led to some new and interesting results †.

This fauna is not very numerous in species; but the number of individuals of the different species is enormous. I give here an enumeration of the species that have been found:—

* Translated from the 'Biologisches Centralblatt,' Band ii. p. 299.

† Literature:—

W. Lilljeborg ("Beskrivning &c.," Öfversigt af K. Vetensk. Akad. Förh. 1860) described the genera *Bythotrephes* and *Leptodora*, which are peculiar to this fauna. (*Bythotrephes* was first discovered by Leydig in 1857, in the stomachs of *Coregoni* from the Lake of Constance; he erroneously placed its habitat in the depths of the lake.)

From 1861–1865 G. O. Sars described numerous pelagic Entomostraca in the Norwegian lakes. ("Om Crustacea Cladocera," Förh. i Vidensk. Selsk. Christiania, 1861; 'Om en i Sommeren 1862 foretagen zoologisk Reise,' Christiania, 1863; 'Norges Fervands Krebsdyr,' Christiania, 1865.)

In 1866 Schödler ("Cladoceren des Frischen Haffs," Wiegmann's Archiv, 1866) described *Daphnie* which he had captured in the Frischen Haff.

In 1867 P. E. Müller ('Dänmark's Cladocera,' 1867; "Cladocères des grands lacs Suisses," Arch. des Sci. Phys. et Nat. Genève, 1870) ascertained the presence of this fauna in the Danish lakes; in 1868 he also found it in the Swiss lakes.

In 1871 Frič investigated the distribution of these Entomostraca in the Bohemian lakes ("Fauna der Böhmerwaldseen," Gesellsch. der Wissensch. Prague, 1871).

From 1874 to 1879 I myself investigated them in the Swiss lakes ("Matériaux pour la faune profonde du lac Léman—Faune pélagique XXXII., Flore pélagique XXXIII., Transparence de l'eau VII. et XXXVIII.," Bull. Soc. Vaud. Sci. Nat. tomes xiii. & xiv. Lausanne, 1876; "Variations de la transparence de l'eau," Arch. des Sci. Phys. et Nat. lix., Genève, 1877).

From 1874 to 1879 A. Weismann published his fine memoirs upon the natural history of the Daphnidæ ("Beitr. zur Naturg. der Daphniden," Zeitschr. für wiss. Zool., 1874–79), founded upon his investigations in the Lake of Constance. In 1877 he gave, in a popular discourse, "Das Thierleben im Bodensee" (Lindau, 1877), an excellent general description of the different faunas that inhabit the lake, and especially of the pelagic fauna.

In 1877 Pavesi discovered the marine fauna in the Italian lakes (Bull. entom. 1879; Rendiconti R. Ist. Lomb. ser. 2, xii. f. 11, 12, 16).

In 1879 Brandt collected these forms in the Gotschäl lake, in the Caucasus (Bull. Acad. St. Pétersb. 1880).

S. T. Smith has detected them in Lake Superior, in North America.

G. Asper ('Gesellsch. kleiner Thiere der Schweizer. Seen,' Zurich, 1880) studied the pelagic and abyssal fauna of the different Swiss lakes.

OSTRACODA : *Cypris ovum*.

CLADOCERA : *Sida crystallina*; *Daphnella brachyura*; *Daphnia pulex*, *D. magna*, *D. longispina*, *D. hyalina*, *D. cristata*, *D. galeata*, *D. quadrangula*, *D. mucronata*; *Bosmina longirostris*, *B. longispina*, *B. longicornis*; *Bythotrephes longimanus*; *Leptodora hyalina*.

COPEPODA : *Cyclops coronatus*, *C. quadricornis*, *C. serrulatus*, *C. tenuicornis*, *C. brevicornis*, *C. minutus*; *Heterocope robusta*; *Diaptomus castor*, *D. gracilis*.

If we were to cite all the animals which are found in the pelagic region of the lakes we should have to add the insectivorous fishes which feed upon these little Entomostraca, especially the *Coregoni*, and, further, the predaceous fishes (trout, pike, &c.) which attack the *Coregoni*; we should also have to add the Infusoria (*Vorticella convallaria*) which live upon the pelagic Algæ; and, finally, we should have to cite the animals which dwell far from the shores or rise from the bottom, and are thus found occasionally in the pelagic region, such as *Atax crassipes* (Pavesi, Asper), larvæ of Diptera, and *Piscicola geometra* (Forel). All these animals, however, appear only occasionally and as accessories in the pelagic fauna, which in reality embraces only the above enumerated Entomostraca*; these alone show the peculiar characters of pelagic animals.

In its general features the pelagic fauna is similar in all the countries and lakes of Europe that have as yet been investigated, from the lakes of the plains to those of the Alps, and from the Scandinavian countries to Southern Italy and the Caucasus. It is, however, seldom represented in any one lake by all the animals of the fauna. Thus, for example, the pelagic fauna of the Lake of Geneva in the years 1874-78, during which I investigated it, only possessed the following species:—*Diaptomus castor*, *Daphnia hyalina*, *D. mucronata*, *Bosmina longispina*, *Sida crystallina*, *Bythotrephes longimanus*, and *Leptodora hyalina*. From this point of view Pavesi has very carefully examined the Italian lakes, and given for each of them a table of the species captured. In estimating these tables, however, Weismann's observations must be taken into account. This naturalist has shown that the different species of Cladocera present a yearly periodicity; that during many seasons they disappear more or less com-

* Perhaps *Atax crassipes*, which Pavesi sometimes observed in the pelagic region of the Italian lakes, and which Asper detected in the Lake of Zurich, must be regarded as a species belonging to the pelagic fauna. It is a swimming water-mite, and, according to these observers, the specimens captured were almost transparent.

pletely from the waters they inhabit, and can only be found in the state of resting-eggs; that this period during which the animals disappear varies according to the different species, occurring for one in the summer, for others in the winter, spring, or autumn. According to this a revision of the pelagic population of a lake, if it is to be complete, must be drawn up on the results of numerous observations made at different seasons of the year.

The characters common to the animals of the pelagic region are due to their mode of life. They must swim incessantly without ever being able to rest upon a solid body; and instead of any organ of adhesion they possess a highly developed natatory apparatus; their specific gravity, which is nearly the same as that of the water*, enables them to swim about in the water without any great muscular exertion. They are rather sluggish animals, and escape the enemies that pursue them rather by their transparency than by their activity; they are, indeed (and this is their characteristic peculiarity), perfectly transparent, like crystals; and only their strongly pigmented black, brown, or red eye appears distinctly. This nearly perfect transparency of the pelagic animals may be regarded as a mimicry acquired by natural selection; only the animals which are as transparent as the medium in which they live have held their own.

They feed upon vegetable or animal structures; some feed upon pelagic Algæ (*Anabaena circinalis*, *Pleurococcus angulosus*, *P. palustris*, *Tetraspora virescens*, *Palmella Ralfsii*); the rest upon animal prey, eating the smaller and weaker species which live in the same water.

The pelagic animals perform daily migrations, as was found independently by Weismann and myself in 1874: during the night they swim at the surface; during the day they descend into the depths. Frič thought that in the Bohemian lakes he found that the different species selected a particular depth at which they preferred to dwell; but neither Pavesi nor myself have been able to ascertain that there was any such constancy of habitat. The different species form groups or flocks, in which the net obtains an abundant booty; but, at least in the great Swiss lakes, these associations of animals of the same species maintain no definite and permanent position.

As regards the greatest depths at which they are met with, I have captured them in the Lake of Geneva as far down as

* They are a little heavier than the water; and when they die the dead bodies sink to the bottom of the lake and then form an important part of the food of the fauna of the depths.

100 and even 150 metres; at these great depths, however, I have only found *Diaptomus*.

On account of these migrations Weismann regards them as nocturnal animals which keep at the extreme limit of light; their optic nerve would suffer under the influence of too bright a light, and they therefore descend into the deep water so soon as the light of the sun or moon becomes too strong. Nevertheless they must still see in order to be able to pursue their prey; and they therefore only descend to the point where their generally well-developed eyes enable them to find their nourishment. Weismann justly remarks that in these migrations they traverse daily a colossal stratum of water, in which they may find sufficient nourishment, sparingly as this may be distributed in the comparatively clear water of the freshwater lakes.

But what is the limit of light in freshwater lakes? I demonstrated in 1877 that the transparency varies with the seasons of the year; in the Lake of Geneva a shining object immersed in the water disappears (when the conditions of illumination and transparency are most favourable) when it is in a stratum of water of a depth of 16-17 metres. Photographic investigations with paper sensitized with chloride of silver had proved to me in 1874 that the limit of absolute darkness in the Lake of Geneva lies at a depth of 45 metres in summer and of 100 metres in winter. Asper, using much more sensitive plates (with emulsion of bromide of silver), in August 1881, found that the rays are still efficacious at 90 metres and more in the Lake of Zurich. All this, however, tells us nothing as to the limit of absolute darkness for the retina and especially the visual nerves of the low animals.

What is the origin of this pelagic fauna? Does it depend upon a local differentiation? Have the palustrine or fluvial Entomostraca, those of the littoral region of the lakes, become transformed in each lake into pelagic species or varieties? To this last question we can with certainty answer in the negative. The remarkably wide distribution of this fauna, the almost complete identity of the pelagic Entomostraca in all the European lakes, from the Scandinavian to the Swiss, Italian, and Armenian, speak in favour of a common origin and distribution.

But how has this distribution been effected? Active migration from one lake to another is not admissible, both on account of the difficulty of communication between the different lakes, and because of the slowness and inactivity of the pelagic Entomostraca. On the other hand, passive migration in the state of resting-eggs which may have attached them-

selves to the feathers of migratory birds (ducks, grebes, gulls, &c.) perfectly explains the transference from one lake to another (A. Humbert, Forel). Pavesi has urged against this common origin and mode of distribution the irregularity of the pelagic peopling of the different Italian lakes, as many species are deficient in certain lakes while they occur in neighbouring lakes; but this very irregularity seems to me to be in favour of the occasional and accidental mode of distribution that we have just indicated. If we accept this mode of distribution, the differentiation of the pelagic species is no longer necessarily limited to the lake in which we find the animals or to the present geological epoch. This fact is of great importance in the explanation of the pelagic fauna of certain lakes of comparatively recent origin; in the case of our Swiss lakes the glacial period forms an absolute limit, which entirely prevents our accepting a local differentiation of the old Tertiary species and their transformation into the existing species. The pelagic faunas of many Italian lakes of volcanic origin are of a much later date still. But as we are no longer confined to a local differentiation of the autochthonous species, we have more time and space at our disposal for this differentiation.

I believe we must find the cause of the differentiation of the pelagic fauna in the combination of two different phenomena—namely, the daily migrations of the Entomostraca, and the regular local winds of the great lakes. It is well known that on the borders of great masses of water two regular winds prevail, one of which blows at night from the land towards the water, the other by day from the water to the land. The nocturnal animals of the shore-region which swim at night at the surface are at this time driven towards the middle of the lake by the surface-current of the land-wind, sink during the day, being driven away by the light, into the deep water, and thus escape the surface-current of the lake-wind, which would otherwise have carried them again to the shore. Constantly driven further every night, they remain confined to the pelagic region, as they are not carried back again during the day. Thus a differentiation takes place by natural selection, until at last, after a certain number of generations, there remain only the wonderfully transparent and almost exclusively swimming animals which we know. When this differentiation has once taken place, the pelagic species is conveyed by the migratory water-birds from one country to another and from one lake into another, where it reproduces its kind if the conditions of existence of the medium are favourable. In this way we may find the pelagic Entomostraca in lakes which are too small to possess the alternation of winds, the

animals having been differentiated by the action of the winds in other larger lakes.

In this way we can easily explain the differentiation of most pelagic species, with the exception of two; and these are the finest and most interesting of the pelagic Entomostraca—namely *Leptodora hyalina* and *Bythotrephes longimanus*. These two Cladocera are not related to the freshwater species which form the littoral faunas of the lakes, or the palustrine and fluviatile faunas*; and therefore we cannot explain their origin by differentiation of the littoral forms. For these two species we must therefore, like Pavesi, seek a *marine origin*. *Bythotrephes* would be derived from an ancestor which was common to it and to *Podon*, its nearest ally, as, indeed, Leydig has already indicated. *Leptodora*, on the contrary, according to Weismann's view, would have branched off from a primæval Daphnid, of whose direct descendants nothing further is known.

But how could the passage from salt into fresh water be effected? Pavesi supposes that this may have taken place by the closing of a fjord, and its gradual conversion into a freshwater lake, so soon as it was separated by a bank from the sea. This is possible; and we have examples of the same kind in certain marine forms which occur in the freshwater lakes of North Italy and Scandinavia. But how if this transition has not taken place by passive migration and transference into lagoons which were constantly becoming less salt? For the decision of this question we have still no reliable materials. But so soon as the adaptation to fresh water had been effected, the distribution of these forms of marine origin took place in the same way as with other pelagic freshwater forms, and thus these two forms would be introduced into lakes which were never in direct communication with the sea.

In conclusion, we might draw a parallel between the pelagic fauna of freshwater lakes and that of the sea. The analogies are numerous and of great interest; but they are so patent that it is superfluous to dwell upon them particularly. The general facts are the same or very similar; the distinction lies chiefly in size and number. In the sea all is large; in our lakes every thing is of small and restricted dimensions—not only the number and size of the individuals, but also the number of species, the extent of their migrations, and their range of distribution.

* G. Joseph has discovered, in two large caves of Carinthia, a second species of the genus *Leptodora*, *L. pellucida*, which differs essentially from the *L. hyalina* of the pelagic lake-fauna by the absence of eyes. It is the only Cladocere that occurs in the cave-fauna (Berl. entom. Zeitschr. xxvi. 3, 1882).